SEXUAL DIFFERENCES IN THE POST-BREEDING MOVEMENTS AND HABITATS SELECTED BY WESTERN TOADS (*BUFO BOREAS*) IN SOUTHEASTERN IDAHO

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    ABSTRACT: We used radio-telemetry to study the movements and habitat use of Western toads (*Bufo boreas*) in the Targhee National Forest in southeastern Idaho. Eighteen toads (10 male and 8 female) that bred in a seasonally flooded pond, were fitted with radio-transmitters, tracked, and their movements mapped and analyzed with global positioning and geographic information systems. We also analyzed their patterns of habitat selection at micro- and macro-scales by comparing sites used by toads with randomly selected sites. After breeding, two male and six female toads left the breeding pond and used terrestrial habitats extensively. Male and female toads showed different patterns of movement and habitat use, although all toads seemed to behave in ways that reduced loss of body water (e.g., such as traveling on nights of high humidity). Male toads traveled shorter distances from the pond than females (581 ± 98 m and 1105 ± 272 m, respectively). Female toads used terrestrial habitats extensively and were selective of cover types (e.g., shrub) that provided greater protection from dehydration. Female toads also preferred certain habitat edges and open forests over forests with closed canopies or clearcuts. Information from this study can assist land managers in establishing protective buffers and managing forests for the protection of toad populations.

    Key words: Amphibians; Forests; Habitat selection; Movements; Western toads

Many amphibians require both wetland and terrestrial habitats. After breeding, adults use terrestrial habitats for dispersing, foraging, and hibernating (Semlitsch, 1998; Sinsch, 1988), and may travel kilometers overland in search of resources (Campbell, 1970; Pilliod et al., 2002; Sinsch, 1988, 1989). In a heterogeneous landscape, structural differences in cover among vegetative stands (patches) create differences in thermal and moisture conditions (Campbell and Norman, 1998; Chen et al., 1993). Because amphibians are wet-skinned ectotherms, their chances for growth and survival depend upon their selection and use of different habitats (Huey, 1991). Human activities that remove large amounts of cover (e.g., timber harvest) also create large changes in the thermal and moisture conditions of patches (Chen et al., 1993). These changes may reduce the ability of amphibians to disperse across the landscape (Rothermel and Semlitsch, 2002), leading to a reduction of their abundance and diversity (Bennett et al., 1980; Corn and Bury, 1989;

deMaynadier and Hunter, 1995; Pough et al., 1987).

    Western toads (*Bufo boreas*) occur in forested habitats throughout much of western North America, and are declining throughout much of their range (Loeffler, 1997; Muths and Nanjappa, in press; Peterson et al., 1992). In the southern Rocky Mountains portion of its range, *Bufo boreas* is a Candidate for listing as "endangered" by the U.S. Fish & Wildlife Service (http://ecos.fws.gov/species_profile/SpeciesProfile?spcode=D026), and is listed as endangered, protected, sensitive, or of special concern in the Rocky Mountain States (Idaho Conservation Data Center, 1999; Muths and Nanjappa, in press). Recent evidence suggests that a chytrid fungus is primarily responsible for declines of Western toads in Colorado (Loeffler, 2000), and possibly elsewhere. If human activities that alter habitats cause additional stress to toads, this could also contribute to population declines (Carey et al., 1999).

    Post-breeding Western toads are known to leave breeding ponds for terrestrial habitats and use a variety of habitat types (review by Muths and Nanjappa, in press). They may travel a kilometer or more to forage and reach

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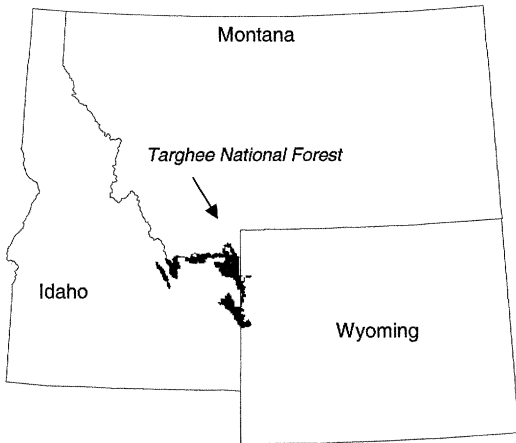[4] Correspondence: e-mail, barteltp@waldorf.edu

FIG. 1.—Study Site Location. The Targhee National Forest is located on the borders of Idaho, Montana, and Wyoming. Stamp Meadows is located near the center of the forest.

a hibernaculum, feeding primarily on ground-dwelling insects and arthropods. A focal study conducted in Idaho showed that toads were active night and day (S. R. Sullivan, unpublished data). They traveled mostly at night when humidity was higher, but fed mostly during the day and basked in the sun. This suggests the importance of selecting protective daytime retreat sites when moisture conditions are potentially stressful.

In 1993 and 1995, we studied a population of Western toads that inhabited an area known as Stamp Meadows in southeastern Idaho. We followed the movements and recorded the habitats used by post-breeding adults. Our objectives were to characterize the movements and terrestrial cover types selected by post-breeding adults, and to describe this information in ways that can be easily used by land managers to better conserve toad populations. Because this was an exploratory study (Jaeger and Halliday, 1998), we broadly hypothesized that toads would select habitats with protective retreat sites and abundant food sources.

MATERIALS AND METHODS

Study Site

Stamp Meadows is located on the Targhee National Forest in southeastern Idaho (Fig. 1). It is a grassy meadow surrounded by a mosaic of coniferous habitats (*Pinus*, *Picea*, and *Abies*) that have been modified by logging. In spring of normal to wet years, water collects to form a large (10–15 ha) pond, bordered by willows (*Salix* spp.), aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*). In 1993 and 1995, toads bred in this pond from late May through mid-June. During this time, we captured and uniquely marked (Martof, 1953) 68 toads and made standard measurements (sex, mass, snout–urostyle length [SUL]) for each toad. This site was not used for our research in 1994 because of drought conditions.

Weather Conditions

To characterize and compare seasonal weather conditions for 1993 and 1995, we used data collected at the U. S. Department of Agriculture Forest Service, Island Park Ranger District Office (approximately 8 km south of the study site), as well as at the study site. For the latter, we recorded 1-m air temperature (T_a) and relative humidity (RH) with a CR10 data logger[1] (Campbell Scientific, Inc., Logan, Utah), equipped with a PCRC-11 humidity transducer (Phys-Chem Scientific Corp) (<3% error from 12–100% RH, <1% error from 25–94% RH). The data logger was placed near the center of the study site, hidden from public view.

Movements of Toads

Field measurements.—We used radio-telemetry to follow the movements of 18 toads, chosen opportunistically from the total 68 toads we caught. We used a plastic belt to secure a 1.85 g BD-2GT transmitter (Holohil Systems, Ltd., Carp, Ontario, Canada) to each toad. The range of initial toad masses was 30–65 g (47.9 ± 2.7 g) and the mass of these radio packages ranged 2.8–6.2% (4.1 ± 0.2%) of toad masses, well below the recommended limit of 10% of body weight (Berteaux et al., 1994). This attachment method had previously demonstrated no measurable effects on toad behavior (Bartelt and Peterson, 2000; Murry and Fuller, 2000; S. R. Sullivan, unpublished data). We located and followed the movements of these toads for 7–17 wk (late May through mid-August) with a Telonics (Mesa, AZ) *TR-2*

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[1] Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

TABLE 1.—Habitat composition at Stamp Meadows, Targhee National Forest, Idaho. Average amounts of ground and canopy cover and density of anthills among the different types of cover patches.

Cover type	Patch area (ha) ($\bar{x} \pm$ SE)	% of total area	Ground cover					Canopy cover		Anthills (avg #/transect)
			Herb	Soil	Debris	Litter	Moss	Shrub	Tree	
Closed forest	8.7 ± 1.1	43.7	29.3	8.3	42.9	19.4	5.2	30.1	53.1	1.6
Open forest	12.9 ± 4.8	16.2	50.7	11.6	26.8	11.9	2.5	15.2	26.7	3.4
Clearcut										
(1 yr)	13.2 ± 3.5	4.7	11.5	18.3	31.2	37.4	1.4	6.0	3.0	0.3
(10–15 yr)	9.9 ± 2.1	6.2	42.0	11.9	28.3	17.8	1.4	10.2	0.7	2.8
(25 yr)	8.0 ± 0.8	22.5	36.4	13.5	40.7	6.5	8.7	37.0	15.1	1.8
Shrub	4.1 ± 0.8	2.2	46.1	7.4	29.0	17.5	0.1	44.6	8.6	4.1
Meadow	3.6 ± 0.8	4.4	67.0	12.8	19.1	2.0	0	2.0	3.9	1.8

receiver and H-type directional antenna. Sixteen toads (eight breeding pairs) were radio-tagged in early spring; two toads were tagged mid-season of 1993.

To increase the independence of data collected on individual toads, we located each toad every 2–5 d. The UTM coordinates (NAD83 datum) of each site were recorded with a Trimble® Basic+ global positioning system (GPS) receiver (Sunnyvale, California). The GPS data were post-corrected (accuracy of ±3–5 m RMS) and imported into a geographic information system (GIS).

Habitat Selection

The selection of habitats by animals may vary by gender and by spatial scales (e.g., Bergin, 1992; Klaver, 2001). To capture this variation, we tested patterns of habitat selection among male and female toads and at three different spatial scales.

Field measurements.—We measured prey abundance and the structure of terrestrial habitats used by toads at macro- (multihectare patches) and microhabitat (≤ 1 m^2) scales. Habitat structure was classified into ground cover components (herbaceous, litter, bare soil, woody debris, moss) and canopy cover components (tree and shrub), quantified as percent cover.

Macrohabitats.—We produced a cover map from 1:15,840 stereographic aerial photographs (provided by Targhee National Forest) by delineating 93 generally homogeneous habitat patches within a 8.2 km^2 area (an area large enough to contain all toad movements). We categorized the study area into five broadly

defined cover types (Table 1); "clearcut" type was subdivided, based on approximate years since harvest (1 yr, 10–15 yr, and ≥ 25 yr). The percent ground and canopy cover for each habitat patch was quantified with an ocular tube (James and Shugart, 1970) every 2 m along randomly placed 200-m transects (2–4 transects per patch, depending on patch size). Conifer plants with a diameter at breast height (DBH) <10 cm (and often with branches near or on the ground) were classified as "shrub." Finally, because harvester ants (Pogonomymes spp.) were important food items for toads (Bartelt, 2000), and to test the relative importance of prey abundance in habitat selection by toads, we estimated the relative abundance of ants among habitat patches by counting the number of anthills within 2 × 200 m belt transects; these were run concurrently with the vegetation transects.

After completing the field transects, we classified the patches according to dominant cover type. Patch size ranged from 2–35 ha. Many patches were highly irregular in shape, and distance from the interior of a patch to its edge ranged from 20 m to almost 300 m. Nearly half of the study area was covered with closed conifer forest ($\geq 50\%$ tree cover); the remaining habitat patches were dominated by open conifer forest (<50% tree cover) or habitats with <10% tree cover (clearcuts varying in age from 1–10 yr, meadows, or shrub). Shrub cover in patches classified as "shrub" was dominated by broadleaf species, such as Salix, Vaccinium, and Sambucus, with some Juniperus; shrub cover in forested patches was dominated by conifer saplings and Juniperus.

Water made up about 2% of the study site area; it was contained within a single pond and a temporary stream that fed the pond. Both the pond and stream dried by midseason, after which no standing water was available to the toads.

Microsites.—A microsite was the spot on the ground where we found a toad. We characterized each microsite by recording its type of ground cover and canopy cover and measured its T_a and RH with an electronic psychrometer equipped with a dry and wet thermocouple (Check-It Electronics, Inc., Elizabeth, New Jersey) and a Solomat Modumeter 2000® (Zellweger Analytics, Flowery Branch, Georgia).

Microhabitats.—We measured microhabitat structure with a 1-m^2 quadrat (divided into 100, 10-cm^2 areas), centered on each microsite (Dueser and Shugart, 1979; Reinert, 1984), and used a point-intercept method (Levy and Madden, 1933) to estimate ground and shrub cover. We used a concave spherical densiometer to estimate tree canopy cover. Spherical densiometers may produce biased estimates of forest canopy cover (Cook et al., 1995; Nuttle, 1997), but fine differences in canopy cover were not an important factor in this study. We recorded the distance between the animal and the nearest source of protective cover (e.g., burrow, shrub, hollow log), and noted its size and type; if the toad was well hidden in some type of cover, we recorded the distance as 0 m.

Data Analysis

Movements.—We used circular statistics (Batschelet, 1981; Zar, 1999) to test for significant ($\alpha = 0.05$) linearity and bimodal patterns (i.e., data with two modes lying at opposite ends on the diameter of a circle), and a GIS to analyze movement patterns among habitat patches. To analyze general environmental conditions under which toads moved across the landscape, we used t-tests to compare T_a and RH conditions during nights when toads moved shorter distances (<50 m) from their previous sites with conditions during nights when toads traveled longer distances (≥ 50 m).

Habitat selection.—For all of our analyses, we tested the null hypothesis that toads used terrestrial habitats proportionally to availability (Sampling Protocol A, Manly et al., 2002; $\alpha =$ 0.05). To best detect patterns of habitat selection, we conducted multiple analyses at micro- and macroscales and restricted our analyses to cover types used by toads during daytime hours (0600–2100). To increase the power of our analyses, we pooled data for 1993 and 1995 because analyses failed to detect significant differences in patterns between these years (Schooley, 1994). All analyses of habitat selection were completed with SAS 8.2 software (SAS Institute, Cary, North Carolina).

Categorical patch selection.—Following Manly et al. (2002) and Neu et al. (1974), we calculated a standardized "Selection Index" for male and female toads to estimate the likelihood that toads will select particular patch types. A "Selection Index" for each patch type was computed by dividing its proportion of use by the proportion of times it was randomly selected.

Macrohabitats.—To analyze habitat selection as toads moved across the landscape, and in a way that reflected their use of vegetative structure, we used discrete choice analysis to calculate maximum likelihood estimators of cover types within the patches. Discrete choice analysis is a multivariate extension of the habitat analysis of Arthur et al. (1996) when available habitat changes. To estimate habitat availability at this scale, we used Arc/INFO (ESRI, Redlands, California) to populate the cover map with randomly located points. Each point was located at a random polar coordinate within 300 m of a used site; this figure represented a 28.3-ha area surrounding each used site and captured 99% (71/72) of all daily distances (including longer dispersal distances) made by toads in 1993. We used only availability sites of males for analysis of habitat selection in male toads, and availability sites of females for female toads.

Model calculation and selection.—Based on results of descriptive statistics of data compiled from the cover map, we did not include herbaceous cover type into our analysis at the macrohabitat scale. Correlation analysis showed that herbaceous cover was significantly ($P < 0.0001$) correlated with litter, woody debris, shrub, and tree cover ($r = -0.630$, -0.678, -0.339, and -0.547, respectively), and a test of collinearity showed that herbaceous cover accounted for the majority of variance inflation (18.177). In addition, an analysis of

principal components showed that tree, shrub, litter, and soil cover accounted for 92% of the variance in the data.

Using a 30-m digital elevation model (DEM; Gesch et al., 2002) of the study area, we added slope (expressed as percent) and aspect (transformed into continuous variables, sine aspect [SINASPECT] and cosine aspect [COSASPECT]) to the set of predictor variables, as these factors also would affect potential insolation and conditions of toad habitats. We modeled habitat selection as linear combinations of all variables:

Tree + Shrub + Litter + Soil + Moss
    + Debris + Anthills + Slope + Sinaspect
    + Cosaspect

and of these noncollinear variables:

Tree + Shrub + Litter + Soil + Slope
    + Sinaspect + Cosaspect

We used Akaike Information Criterion (AIC) and Receiver Operator Curve (ROC) values to select the best models (Burnham and Anderson, 1998).

Edge effects.—Because forest edges affect amphibian abundance (deMaynadier and Hunter, 1998), we used χ^2 to test for selection among three different types of edges: hard (e.g., forest/clearcut), soft (e.g., forest/shrub), or none (>50 m from an edge). We also used a straight-line distance calculation (NEAR function in Arc/INFO) to measure the distance of used and random sites from the nearest edge, and used a general linear model (GLM) to test whether toads used sites closer to edges than expected.

Microhabitats.—For these analyses, habitat availability was estimated in 1995 by repeating all microhabitat measurements at a random polar coordinate within 50 m of each used site. This distance captured 86% (62/72) of all daily distances traveled by toads in 1993 and better represented finer scale habitat use by toads. Habitat availability was not measured with this method in 1993 and so such data for 1993 are not included in this paper.

Correlation analysis showed no collinearity among these data, so all cover types were used. Tests of microhabitat selection were completed with a 2 × 7 MANOVA (used versus random across seven cover types). To meet assumptions of normality, percent values for these data were arcsine transformed (Zar, 1999).

Microsites.—Clear distinctions between the cover types "litter" and "debris" at microsites often were difficult, so data for these cover types were combined at this scale. We conducted these analyses with a 2 × 6 MANOVA. Small sample sizes for some toads prevented us from completing individual microhabitat and microsite analyses for all toads.

RESULTS

Average monthly temperatures (May–September) for 1993 ranged 16.4–19.7 C ($\bar{x} \pm$ SE = 18.2 ± 0.9 C) and total precipitation was 25.7 cm. Weather conditions for 1995 were similar to those of 1993; average monthly temperatures ranged 12.4–26.1 C ($\bar{x} = 21.2 \pm$ 2.1 C), and total precipitation was 26.9 cm.

Numbers of Toads and Observations

We made 357 observations of 18 toads (104 observations of 6 toads between 30 May–30 August 1993; 253 observations of 12 toads between 31 May–10 August 1995; 10 toads were males and 8 were females. At capture, male toads weighed significantly less than female toads (42.8 ± 3.0 g and 54.5 ± 2.9 g, respectively: $t_{16} = 2.767$, $P = 0.007$), and had a significantly shorter SUL (69.9 ± 2.1 mm and 78.4 ± 2.0 mm, respectively; $t_{16} = 3.211$, $P = 0.005$). There was no difference in the average mass gained by male and female toads during the study (5.2 ± 1.4 g and 5.1 ± 2.2 g, respectively; $t_{16} = 0.267$, $P = 0.49$). Toad activity was concentrated in and around the pond, with about 60% of all observations occurring within 200 m of the pond, and the remaining 40% occurring at greater distances (Fig. 2).

Movement Patterns

Daily patterns.—The nights on which toads traveled >50 m overland were significantly warmer (11.0 ± 0.5 C versus 9.2 ± 0.8 C; $t_{72} = 2.114$, $P = 0.019$) and more humid (88.8 ± 1.2% versus 79.8 ± 1.8% RH; $t_{72} = 8.261$, $P < 0.001$) than nights when toads were more sedentary (Fig. 3). About 78% of daily toad movements were ≤50 m; 10% were 50–100 m and 12% were >100 m. The greatest single day
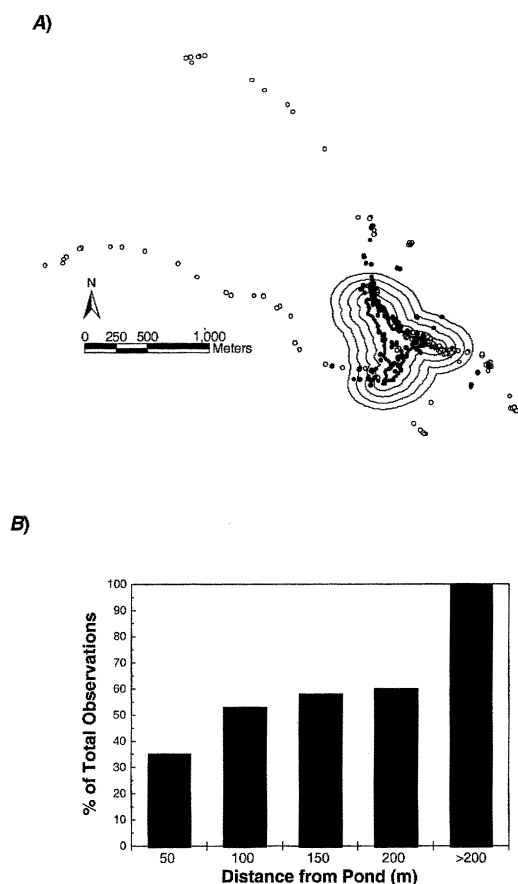
A)

B)

FIG. 2.—Distribution of toad locations around the breeding pond. A) A series of 50-m buffers around the pond are depicted to a distance of 200 m. Two male (filled circles) and eight female (open circles) toads traveled beyond 200 m of the pond. B) About 60% of our observations of toads in terrestrial sites were made within 200 m of the breeding pond.

movements were 416 m and 439 m, traveled by a male on 5 June and 30 July 1995, respectively. Daily distances, averaged over the study period, were 39.2 ± 7.8 m for male toads and 38.9 ± 5.3 m for females, a difference that was not statistically significant ($t_{194} = 0.027$, $P = 0.49$). However, average daily distances changed from June through August, and the pattern of change between male and female toads was significantly different ($\chi^2 = 12.737$; $P < 0.005$) (Fig. 4). Average daily distances traveled by males was less than females in June, but was greater than females in July and August.

Seasonal patterns.—While male and female toads traveled similar distances on a daily
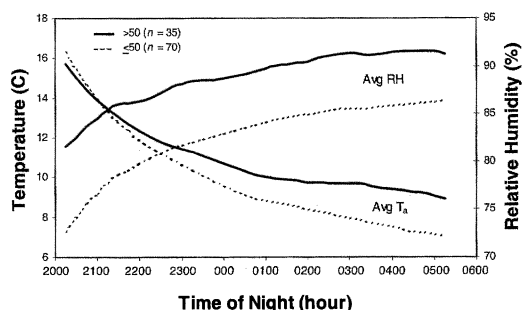

FIG. 3.—Mean nightly air temperature (T_a) and relative humidity (RH) conditions at Stamp Meadows. Bold lines indicate average conditions on nights when toads traveled longer distances (>50 m); dotted lines indicate average conditions on nights when toads traveled shorter distances (≤50 m). Toads traveled longer distances on nights that were warmer and more humid.

basis, they displayed different seasonal patterns of movement. With two exceptions, male toads remained in the breeding pond area, even after the pond dried, but female toads (with two exceptions) traveled away from the pond after breeding. Overall, male toads traveled significantly shorter distances from the pond than females (581 ± 98 m and 1105 ± 272 m, respectively; $t_{16} = 2.306$, $P = 0.041$). The greatest total seasonal distances traveled by a male and a female toad were 0.94 km and 2.44 km, respectively.

The movements of 9 toads (4 males and 5 females) were directionally oriented (i.e., traveled in statistically straight paths; Rayleigh's test, range of r's = 0.5–0.938, range of P's = <0.001–<0.05), and those of three males and one female were bimodal (i.e., repeatedly traveled between two different sites). The movements of the remaining nine toads were not statistically different from random (Rayleigh's test, range of r's = 0.123–0.466, range of P's = >0.2–>0.5). With one exception, toads that moved ≥900 m from the pond traveled in paths that were statistically linear, although their directions of travel differed.

Habitat Selection

Overall, we found toads in terrestrial habitats (i.e., >10 m from the pond) 58.3% (208/357 observations) of the time. Males used terrestrial habitats significantly less often than females (41.5% versus 78%, respectively;

$t_{16} = 2.572$, $P = 0.02$), and both sexes used terrestrial habitats more frequently in July and August when the pond dried. We found toads in all cover types, but different patterns of selection emerged among male and female toads.

Patch selection.—Male toads showed greatest selection for meadow, shrub, and 10-yr clearcut patch types ("Selection Index" in Table 2). Compared to 1-yr clearcuts, male toads selected these three patch types over five, three, and three times, respectively, more often ("Relative Probability"). Female toads showed greatest selection for shrub and open forest patch types; they selected these about 14 and 12 times, respectively, more frequently than 1-yr clearcuts, and 2–3 times more frequently than other patch types.

Macrohabitat selection.—Male toads more often used macrohabitat patches with lesser amounts of litter on slopes with an easterly aspect (i.e., statistically, these patches had a higher utility). For female toads, patches with greater amounts of shrub cover and with a westerly aspect had higher utility (Table 3).

Edge effects.—Female toads selected among edge types differently than was expected and seemed to show a preference for soft edges (Fig. 5). Sites selected by both male and female toads were significantly closer to patch edges than randomly selected paired sites (males: 16.6 ± 1.0 m versus 24.6 ± 1.9 m; $F_9 = 2.24$, $P < 0.02$; females: 24.3 ± 1.7 m versus 34.6 ± 2.5 m; $F_7 = 2.23$, $P = 0.03$).

Microhabitat selection.—Of the 121 observations we made of toads in terrestrial sites in 1995, we made 81 measurements of microhabitats (toads inhabited rodent or other underground burrows for 12 of these observations and were obscured by cover for another 28). Male toads selected sites with less tree cover and greater amounts of bare soil than randomly selected sites, and females selected sites with greater amounts of shrub cover and bare soil (Fig. 6).

Microsite selection.—We found male and female toads sitting on bare soil, and female toads sitting under shrub cover more often than expected if sites were selected randomly (Table 4). Sources of cover (e.g., burrow, woody debris, shrub growth) were also significantly closer to used than random sites (0.66 ± 0.08 m and 1.57 ± 0.1 m, respectively;
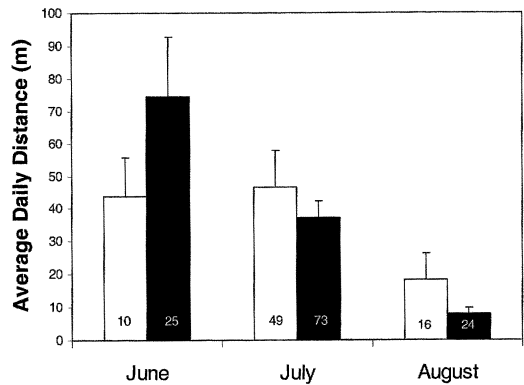

Fig. 4.—Changes in average daily distance traveled by male and female toads at Stamp Meadows during the study season. Toads of both sexes traveled shorter average daily distances as the season progressed, although the rate of decrease for females was greater than for males. The seasonal pattern between male and female toads was significantly ($P < 0.05$) different. Distances ($\bar{x} \pm$ SE) traveled by male and female toads indicated with open and closed bars, respectively. Numbers at bottom of bars indicate n.

$t_{16} = 2.285$, $P = 0.018$). Males sat slightly and significantly farther from cover sources than females (0.87 ± 0.09 and 0.23 ± 0.02, respectively; $t_{16} = 2.26$, $P = 0.04$).

An analysis of microsite conditions showed that toads in terrestrial habitats used microsites that had similar T_as to randomly selected sites (21.6 ± 0.7 C versus 21.7 ± 0.8 C; $t_{16} = 0.017$, $P = 0.494$), but which were significantly more humid ($84.2 \pm 0.9\%$ versus $74.5 \pm 2.9\%$; $t_{16} = 2.255$, $P = 0.02$). This difference in RH was due to terrestrial sites selected by females after they left the pond. Microsites used by male toads had RH measurements similar to randomly selected sites ($83.7 \pm 0.9\%$ versus $81.5 \pm 1.7\%$, respectively; $t_{10} = 0.24$, $P = 0.406$), whereas those used by females were significantly more humid ($84.9 \pm 1.2\%$ versus $65.1 \pm 2.2\%$, respectively; $t_6 = 3.71$, $P = 0.01$).

DISCUSSION

The results from this study support the hypothesis that toads used terrestrial habitats disproportionate to habitat availability. They also support our hypothesis that toads selected habitats with more protective cover; this was a stronger pattern for female toads. Variation in prey abundance was not an important factor.

TABLE 2.—Habitat Selection Index analysis for toads at Stamp Meadows. Male toads were more likely to select patches of meadow, shrub, and older clearcuts. Female toads selected these patches to a greater extent than males, and also were more likely to select open forests. "Relative probability" estimates the probability for selecting a patch type relative to another patch type. In this table, "Relative probability" is based on the "Selection index" for 1-yr clearcut. For example, female toads at Stamp Meadows were 12 and 14 times more likely to select Open forest and Shrub, respectively, over 1-yr Clearcut.

	Total patch count		Proportion of total			
Patch type	Used sites	Random sites	Used sites	Random sites	Selection index	Relative probability
Males						
Closed forest	30	45	0.375	0.563	0.666	1.49
Open forest	0	2	0.000	0.025	0.000	0.00
Clearcut						
1 yr	4	9	0.050	0.113	0.442	1.00
10–15 yr	12	8	0.150	0.100	1.500	3.38
25 yr	0	0	0.000	0.000	0.000	0.00
Shrub	6	4	0.075	0.050	1.500	3.38
Meadow	28	12	0.350	0.150	2.333	5.25
Total	80	80				
Females						
Closed forest	47	64	0.367	0.500	0.734	3.90
Open forest	20	9	0.156	0.070	2.229	11.86
Clearcut						
1 yr	3	16	0.023	0.125	0.184	1.00
10–15 yr	10	11	0.078	0.094	0.907	4.71
25 yr	13	12	0.102	0.078	1.085	5.62
Shrub	27	10	0.211	0.078	2.705	14.05
Meadow	8	6	0.063	0.047	1.340	6.95
	128	128				

Our data suggest that toads moved through, selected, and used terrestrial habitats in ways that allowed them to conserve body water. Terrestrial amphibians, because of their moist skins, risk desiccation as they move across the landscape in search of food, hibernacula, or new water sources. Huey (1991) argued that basic physiological needs of animals were major factors explaining patterns of habitat

TABLE 3.—Results of discrete choice analysis to calculate maximum likelihood estimates that toads selected particular cover types as they moved across the landscape. Male toads showed lesser utility for litter and greater utility for sites with an easterly aspect. Female toads found greater utility for shrub canopy cover and for slopes with a westerly aspect. Only parameter estimates that were significant (P < 0.05) are listed here.

Sex	Cover type	Parameter estimate	SE	P	Odds ratio
Male	Litter	−0.024	0.010	0.0147	0.976
	Sinaspect	0.304	0.154	0.0484	1.356
Female	Shrub canopy	0.018	0.004	<0.0001	1.018
	Slope	0.060	0.017	0.0005	1.062
	Sinaspect	−0.485	0.201	0.0160	0.616

selection and use. Tracy et al. (1993) showed that, in the laboratory, conserving body water was a higher priority for toads than achieving a warm body temperature. Our results are consistent with those of Huey (1991) and Tracy et al. (1993).

Movements

Toads moved mostly during humid nights when high relative humidities reduce rates of evaporative loss (Campbell and Norman, 1998). They also traversed long distances through upland habitats, relative to their size and vagility. There are other examples where this or a related species has traveled ≥1 km from their breeding sites. For example, Campbell (1970) observed that many Western toads seasonally migrated 0.9 km between a traditional breeding site and a communal hibernaculum. Similarly, Sinsch (1988, 1989) observed European toads (*Bufo bufo*) traveling about 1 km between a traditional breeding pond and hibernaculum. Muths (2003) also

A)

B)

recorded movement distances for Colorado Western toads similar to those in our study.

We are unsure why male and female toads traveled different total distances, but suspect it is related to differences in site fidelity and reproductive needs. In Europe, more than 90% of male natterjack toads (*B. calamita*) showed strong fidelity to their site of first breeding, whereas female toads did not (Sinsch, 1992). Remaining at or near a breeding pond may give males a competitive advantage when females arrive to breed in the spring.

Differences in reproductive needs may also be important. Anurans place large amounts of biomass into an egg clutch, and some anurans at high elevations may spend two or more seasons feeding to produce another clutch (Turner, 1958, 1960). To facilitate the production of another clutch, female toads may be
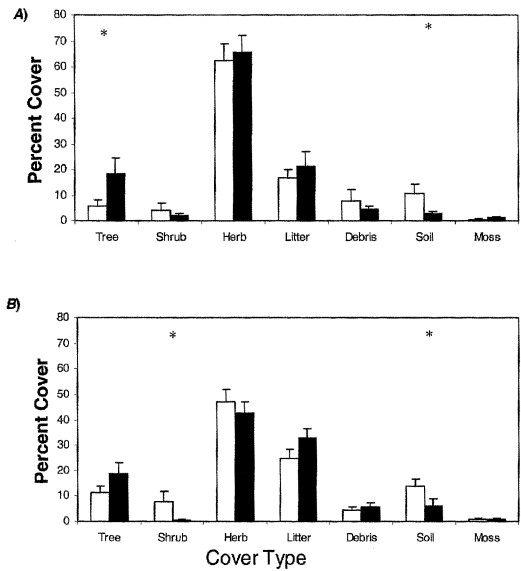
A)

B)

FIG. 6.—Microhabitat selection by Western toads at Stamp Meadows. At this scale of habitat selection, male toads (A) selected sites with significantly less tree cover and females (B) selected sites with significantly greater shrub cover. Toads of both sexes selected sites with significantly greater amounts of bare soil. Frequencies of used and randomly selected sites indicated by open and closed bars, respectively. Significant differences ($P < 0.05$) are indicated with an asterisk (*).

traveling farther to obtain better foraging. In addition, because they are larger, they may have the additional water storage capacity that facilitates longer journeys. Similar gender differences in movement patterns were observed in Columbia spotted frogs (*Rana luteiventris*) in Idaho (Pilliod et al., 2002), where larger females traveled farther distances than males or smaller females.

Habitat Selection

Toads have a number of adaptations for terrestrial life, including an ability to store water in their lymph sacs and bladder (Boutilier et al., 1992) and an ability to withstand relatively high amounts of dehydration (Shoemaker et al., 1992). However, because they have little physiological control over evaporative water loss, toads need to periodically rehydrate and select protected sites that conserve body water (Carey, 1978; Tracy et al., 1993). Toads can absorb moisture from wet substrates (Lillywhite and Licht, 1974), and we

TABLE 4.—Characteristics of microsites selected by toads at Stamp Meadows. Average (± SE) frequency (%) that toads selected microsites dominated by different cover types, compared to same measurements made at random microsites.

	Canopy cover		Ground cover			
	Tree	Shrub	Herb	Debris/Litter	Soil	Moss
Males:						
Used	26.4 ± 2.4	8.3 ± 5.3	52.2 ± 14.1	15.6 ± 2.5*	29.5 ± 5.3*	1.8 ± 0.3
Random	37.2 ± 10.3	2.8 ± 1.8	48.6 ± 9.3	39.6 ± 5.7	11.8 ± 5.1	0.0 ± 0.0
Females:						
Used	19.4 ± 11.0	35.6 ± 5.9*	38.4 ± 14.3	25.9 ± 8.4	35.7 ± 9.2*	0.0 ± 0.0
Random	30.2 ± 8.3	8.2 ± 6.1	32.2 ± 18.8	32.2 ± 18.7	12.9 ± 4.5	0.0 ± 0.0

* Significant differences ($P < 0.05$).

often observed them sitting in contact with damp soil, walking through dew-laden grass in the morning, and emerging from a burrow to sit in rain puddles.

Toads that left the breeding pond did not have standing water for rehydration and seemed to select more carefully and use habitats that reduced rates of water loss. Although most of these toads showed patterns of macrohabitat selection, only five showed patterns of microhabitat selection and these patterns were not consistent. Within the limits of our sample size, this suggests that toads selected habitats with available cover, and then used the cover in ways that met their immediate needs for thermoregulation (e.g., basking) or conserving body water (e.g., sitting in underground burrows or shaded, moist soil).

Patterns of habitat selection were more defined for females than males and included patches or sites with greater amounts of shrub cover. The low and dense structure of shrub cover and similar cover types may facilitate water conservation in toads. If so, breaks in the shrub canopy that were warmed by the sun, plus large accumulations of litter and coarse woody debris, probably provide the warm, moist conditions preferred by wet-skinned ecto-therms (Tracy et al., 1993). Westerly slopes also may enhance such favorable conditions in these cover types. For example, the large numbers of ants we observed in these habitats would have provided an important food supply, especially for females producing a clutch of eggs and in August, when they were preparing for winter. The warm moist conditions of these sites also would facilitate growth by allowing them to remain at higher body temperatures (Lillywhite et al., 1973).

Dehydration probably was not a problem for toads that remained in the vicinity of the pond. They basked on saturated soils along the pond edge, used a variety of habitats and microsites adjacent to the pond, and frequently returned to the pond to rehydrate. However, when the pond dried, these toads remained in the area and also concentrated their activities in the willows that bordered the pond's edge, basking in sunlit areas or half buried in the damp litter and debris under the shrub cover.

Underground burrows and cavities in logs and stumps were important microsites for toads, regardless of cover type. In addition to providing a secure refuge from most predators, the high humidity of these sites (Campbell and Norman, 1998) reduced the loss of body water from toads, probably to negligible amounts (Tracy, 1976). In the absence of standing water, such sites may be critical for the survival of terrestrial toads.

Coarse measures of tree cover were an important factor in the analyses of habitat selection: toads seemed to prefer macrohabi-tats that were neither excessively shaded nor sunny. For example, closed forests, though moist, may have shaded too much solar radiation for toads to achieve a preferred body temperature (Bartelt, 2000; Lillywhite et al., 1973). In contrast, clearcuts had large amounts of solar radiation, but only small amounts of protective cover, which often was concentrated (e.g., slash piles). Clearcutting begins the process of even-aged forest stands, where almost all cover is removed at once and then allowed to regenerate. Cover in these patches increases as new trees grow, but it periodically is thinned to increase the rate of growth of the remaining trees. These patches generally lack

·vertical stratification and ground cover, except for scattered small pieces of woody debris. Slash piles at the edges of these patches were important to three toads, providing a winter hibernaculum for at least one of these. Hence, "clean" clearcuts (i.e., clearcuts with all slash and woody debris removed) provide even less usable cover for toads.

Some pattern of clearcut use was evident among toads, but small sample size limits any conclusions. Males used clearcuts less often than females, probably because they less often used terrestrial habitats. We observed toads crossing the interior of clearcuts only four times; three of these were during or immediately after periods of rain. We never observed toads to be exposed in a clearcut during sunny conditions, and the path of one toad seemed to be deflected around the boundary of a 1-yr clearcut. The warm, open conditions of clearcuts may be stressful to toads, except during wet periods. When toads used a clearcut, they usually remained along its edge.

Patch edges, especially "soft edges," seemed to be an important habitat for female toads in this study. Edges are boundaries between habitat patches that provide an environmental gradient between the two different patch types (Thomas, 1979). The steepness of the gradient depends on the degree of contrast between the two patch types. Edges in managed forests are common and often steep, but their effects on amphibians have received little attention. In Maine, edges between forest and clearcut patches ("hard" edges) had a measurable negative effect on the abundance of amphibians, especially species that made extensive use of upland areas, including American toads (*B. americanus*; deMaynadier and Hunter, 1998). Increasing numbers of amphibians were trapped with increasing distance into intact forests, and amphibian numbers were lowest at distances 25–70 m (the greatest distance samples were taken) into the clearcut. Similarly, we observed that toads remained most often within 25 m of an edge, and only rarely did we observe toads occupying the interior of a clearcut, where rates of dehydration were potentially high.

Not all edge effects on toads may be negative; edges may also help toads meet their biological needs. For example, variation in microenvironmental conditions at edges are greater than those that exist either in closed forest or clearcuts (Chen et al., 1993), and may provide toads with a greater selection of microsites. The selection of "soft" edges by toads in this study suggests that the microenvironmental gradient along "hard" edges may be too great.

Some patch edges may provide important foraging sites for toads. Edges serve as movement corridors for some insects (Wood and Samways, 1991). Whereas density of anthills generally was not an important factor in toad habitat selection, we observed ants and rodent burrows to be common along edges. This overall combination of resources may allow toads to forage, thermoregulate within a wide variation of temperatures, and replenish body fluids from damp substrates.

Our results show that certain practices can be important in conserving toads. For example, establishing a buffer of 150–200 m (similar to that recommended for amphibians by Semlitsch and Brodie, 2003) around breeding ponds would protect a large percentage of toad movements (e.g., Fig. 1). The size of this buffer may vary among breeding ponds in other areas, but buffers large enough to protect the integrity of the breeding pond and promote connectivity between wetlands and terrestrial habitats will promote the persistence of amphibian populations. In addition, patterns of timber harvest that increase sun exposure, but leave sufficient amounts of cover to provide moist microsites (e.g., the creation of "soft" habitat edges or open forest canopies), may benefit toads. However, drying conditions caused by clearcutting or other timber harvest activities and removing large amounts of woody debris may greatly limit toad movements and habitat use, especially if accentuated by extended dry weather.

A number of inferences from this study need further investigation. To better understand habitat selection by Western toads and how habitat alteration may affect them and other amphibians, we need to move beyond statistical models. Mechanistic models that incorporate habitat selection patterns would support an approach that combines population studies with measurements of variations in thermal and moisture conditions among habitats (Bartelt, 2000; Spotila et al., 1992). We suggest this as a next step in advancing the

understanding of amphibian habitat use and conservation of amphibian populations.

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